

Southwest Fisheries Science Center
Administrative Report H-97-05

**August-September 1996 Reevaluation of Shallow Reef Fish
Populations at French Frigate Shoals and Midway Atoll**

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July 1997

NOT FOR PUBLICATION

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ABSTRACT

Divers again conducted visual surveys of reef fishes at two sites, French Frigate Shoals (FFS) and Midway Atoll (MWAY), in August and September 1996, respectively. Surveys were repeated at the same stations at which fishes were surveyed in July 1992 (at FFS), in August 1993 (MWAY), and in September 1995 at both sites. Nine stations in two habitats (four on inner and outer barrier reefs and five on lagoonal patch reefs) were surveyed at FFS; eight stations were sampled successfully at MWAY. Three divers repeated the identical surveying protocols used during 1992-93: two divers simultaneously tallied all larger-than-recruit-sized (≥ 2 cm standard length, SL) fish individuals, encountered within a band transect or other fixed area of reef, by species or lowest recognizable taxon. A third diver meanwhile estimated the body lengths of a random sample of fishes encountered within the same delimited area. As previously, divers rotated between the two (counting, size estimation) tasks.

At FFS, the numerical densities of total fishes were nominally 15% lower in 1996 than 1995, but estimates were statistically indistinguishable between years. Young-of-the-year (YOY) and other small-bodied (≤ 7 cm SL) post-recruits represented about 56% of total fish counts at FFS in 1996 compared to 43% in 1995. Length frequency distributions differed between 1996 and 1995 as the net result of relatively greater numbers of smaller (1-3 cm) YOY in 1995 and disproportionately more, larger (4-7 cm) YOY and yearlings (7-11 cm) in 1996. Growth of the 1995 year-classes over 11 months (Sep95-Aug96), however, did not result in an increase in overall biomass densities. Standing biomass appeared lower at FFS during 1996 (mean = $0.5-0.6 \text{ kg} \cdot 10 \text{ m}^{-2}$, depending on habitat) vs 1995 ($0.6-1.9 \text{ kg} \cdot 10 \text{ m}^{-2}$), but estimates were statistically indistinguishable between years.

Neither numerical densities nor biomass densities differed between 1996 and 1995 at MWAY. Apparent year-differences in the numerical densities of major trophic levels and feeding guilds ranged from about one-fourth less to one-half greater in 1996. Biomass densities were nominally lower at MWAY during 1996 ($0.8-0.9 \text{ kg} \cdot 10 \text{ m}^{-2}$) vs 1995 (0.9 to $<2 \text{ kg} \cdot 10 \text{ m}^{-2}$), but apparent differences were statistically insignificant. Length frequency distributions differed between 1996 and 1995, with relatively greater numbers of 4-5 cm YOY-sized fishes in 1995 and disproportionately more 7-11 cm yearling-sized fishes in 1996.

Patterns of numbers and biomass at MWAY and FFS are discussed relative to the possible current and future food limitation of Hawaiian monk seals, *Monachus schauinslandi*, at FFS.

INTRODUCTION

The Hawaiian monk seal, *Monachus schauinslandi*, is endemic to the Hawaiian Archipelago, where its present distribution in the Northwestern Hawaiian Islands (NWHI) is restricted to six main breeding populations, including French Frigate Shoals (FFS; 24°N, 166°W) and Midway Atoll (MWAY; 28°N, 177°W). Beginning in 1989 and continuing through 1996, the monk seal population at FFS, where about 30% of all NWHI monk seals currently reside, has declined by 55%. These declines at FFS, particularly of juvenile seals, are thought to be related to decreases in the forage base of monk seals, whose broad diet consists of octopus, lobsters, and shallow-water demersal and reef fishes (DeLong et al., 1984; Craig and Ragen, unpubl. ms.).

In order to evaluate whether reef fish populations had recently declined from prior levels, shallow water reef fishes were surveyed at FFS and MWAY in the early 1990s. Surveys were then repeated at stations previously surveyed by U.S. Fish & Wildlife personnel during 1980-83 (at FFS) and 1980 (MWAY). These repeat surveys were first conducted at FFS in July 1992 (DeMartini et al., 1993) and at MWAY in August 1993 (DeMartini et al., 1994). DeMartini et al. (1996) provides a comprehensive interpretation of baseline vs 1992/93 comparisons at both sites. In general, the numerical densities of post-recruit-sized (≥ 2 cm Standard Length, SL) reef fishes declined by about one-third between the early 1980s and surveys made during the early 1990s. At least at MWAY, these declines included both herbivorous and carnivorous fishes and occurred in both major habitat types (DeMartini et al., 1996). When resurveyed in September 1995, densities at FFS had increased by $> 60\%$ compared to July 1992, and densities at MWAY had nominally increased by 31% over August 1993 (DeMartini and Parrish, 1996). In this report, we update our shallow-water reef fish time series for surveys conducted at FFS and at MWAY during August and September, 1996, respectively.

METHODS AND MATERIALS

Field Surveys

FFS

Surveys were conducted over a 3-day period (August 16-18, 1996). Reef fishes were surveyed at historical ("test") stations using the same recording protocols as those used in July 1992. (In September 1995, the data used for analysis were collected by two, rather than three, persons; three-person datasets were used in 1992 and 1996.) As in July 1992, a total of four test stations on the barrier reef (BR: two inner [Sta. Nos. 7, 8] and two outer [Nos. 4, 6]), and five patch reef (PR) stations (Nos.

5c, 5d, 5e, 5f, 23) were surveyed. Each station was surveyed once; two divers tallied densities on a 500 m² band transect (BR stations) or within a delimited area (PR stations), while a third diver simultaneously characterized the body length distribution (by 1- to 10-cm standard length, SL, classes) of fishes in the same station area. Fishes were tallied by species or lowest recognizable taxon. DeMartini et al. (1993) specifies recording protocols and DeMartini et al. (1996) describes station locations and habitats.

MWAY

Surveys were conducted on 4 days over a 5-day period (September 14-18, 1996). Reef fishes were surveyed at test and other stations using recording protocols identical to those used in August 1993. A total of three test stations on the barrier reef (BR: two Inner [Nos. 14, 21] and one Outer [No. 19]), plus five patch reef (PR) stations were resurveyed. Outer BR station No. 10 was missed because of unsafe diving conditions; thus, 1995-96 comparisons were based on eight stations even though nine stations were surveyed in 1995 (DeMartini and Parrish, 1996). The PRs sampled included test stations Nos. 5, 11, and 17, plus 17A (a reference station used as replacement for test station No. 18; see DeMartini et al., 1994) and a newly surveyed patch reef (No. 6X; similar in area to test station No. 6 and used as its replacement). Use of the two replacement PRs was necessitated by sand burial of PR test stations 6 and 18 in September 1996. DeMartini et al. (1994, 1996) provide additional details.

Data Analyses

Species rankings were used to evaluate assemblage structure. Some species of parrotfishes (adult *Scarus* spp) and surgeonfishes (*Acanthurus* spp) that were at times difficult to distinguish underwater were pooled for analyses. Potential changes in numerical densities were evaluated for total fishes, herbivore and carnivore trophic levels, and each of four carnivore feeding guilds (benthic invertebrate-feeders or "benthic carnivores," corallivores, piscivores, and planktivores). Data limitations restricted analyses of size frequency distributions and biomass densities to total fishes and the two trophic levels. Data were post-classified into trophic levels and carnivore guilds as described by DeMartini et al. (1996). Analyses again focused on higher taxa for two principal reasons: (1) The existing data for fish in the monk seal diet has family and grosser taxonomic resolution; and (2) the statistical power to detect changes $\geq 50\%$ in NWHI reef fish densities using diver visual surveys is generally insufficient at the species level (power = $[1-\beta] < 0.80$ at $\alpha_2 = 0.10$; DeMartini et al. 1996).

Temporal changes (1996 vs 1995) in numerical densities were evaluated using bootstrapped paired-comparisons (Manly, 1991), with data paired by station between surveys. The results of

1,000 iterations were evaluated at $\alpha_2 = 0.10$ (Manly, 1991), and Bonferroni's correction was used to control Type I error in multiple comparisons ($\alpha_{crit} = \alpha/m$, where m = number of comparisons; Manly, 1991, p. 52). Analogous comparisons of size-frequency distributions were made using 2-sample Kolmogorov-Smirnov (K-S) tests (Siegel and Castellan, 1988). Biomass densities were calculated first for each taxon as the cross-product of mean body weight per fish and mean numerical density ($N \cdot 10 \text{ m}^{-2}$), and then summed over taxa. Variances were estimated by the delta method excluding covariances (Seber, 1982, p. 9) because analyses indicated that covariances were trivial. Large-bodied transient predators (sharks and the two jacks *Caranx ignobilis* and *C. melampygus*) were excluded from the biomass estimates.

Bootstrap comparisons were coded in Microsoft Quick Basic 4.5. All remaining analyses used PC SAS v. 6.04 (SAS Inst. Inc, 1990).

RESULTS

Relative Densities

FFS

Count data were log-normally distributed among species. The 10 most numerous species dominated total fish densities (75-79%, depending on habitat) during the August 1996 survey. The top 20 and top 30 taxa contributed 92-93% and 97-98% to total densities, depending on habitat. Within habitats, rankings among taxa were generally similar in 1995 and 1996 (Table 1).

MWAY

The 10 most numerous species dominated total densities (83-86%, depending on habitat) in September 1996. The top 20 and top 30 taxa contributed 93-95% and 97% to total densities. Rankings within habitat generally persisted between 1995 and 1996 (Table 2).

Numerical Densities

FFS

In August 1996, total fish densities averaged 16.8 individuals $\cdot 10 \text{ m}^{-2}$ overall, with herbivores (33% of total) and carnivores (67%) averaging 5.6 fish $\cdot 10 \text{ m}^{-2}$ and 11.2 fish $\cdot 10 \text{ m}^{-2}$, respectively (Tables 1, 3). Herbivores were only slightly less numerous (44% of total) than carnivores on the barrier reef; conversely, carnivores were much more numerous (69%) than herbivores on patch reefs (Tables 1, 3). The benthic carnivore guild dominated numerically in both barrier and patch reef

habitats (33-35% of total fishes; Tables 1, 3). Densities were nearly fivefold greater overall on patch reefs.

Bootstrapped paired-comparisons of densities for pooled (barrier and patch reef) habitats did not differ between 1996 and 1995 for total fishes (an estimated 15% lower in 1996), herbivores (5% lower), total carnivores (19% lower), planktivores (9% higher), corallivores (3% higher), or piscivores (11% lower; Table 3). Only the 1996 decline (38%) in benthic carnivores at patch reefs was statistically significant after P-values were adjusted for multiple comparisons (Table 3). Patterns of density change between August 1996 and September 1995 were qualitatively dissimilar in barrier and patch reef habitats only for corallivores and planktivores (Table 3).

The overall numerical similarities between 1995 and 1996 at FFS included most component taxa. Differences were not apparent at the species level within major functional groups (Table 4).

MWAY

Total densities averaged 19.2 fish 10 m^{-2} overall in September 1996, with herbivores (31% of total) and carnivores (69%) averaging 6.0 and 13.2 fish 10 m^{-2} , respectively (Tables 2, 5). Herbivores were slightly more abundant (51%) on the barrier reef, and carnivores were relatively more abundant (72%) on patch reefs (Tables 2, 5). The benthic carnivore guild dominated numerically in the two habitats (35-41% of total fishes; Tables 2, 5). Fishes were more than threefold denser overall on patch reefs.

Bootstrapped paired-comparisons differed insignificantly between September 1996 and September 1995 for total fishes (an estimated 2% greater in 1996), herbivores (27% greater), total carnivores (6% lower), benthic carnivores (16% greater), and planktivores (28% lower; Table 5). The estimated changes in corallivores (44% lower) and piscivores (24% greater; Table 5) should be considered especially suspect because estimates for these relatively uncommon and patchily distributed (piscivore) fishes are extremely imprecise.

The observed similarities between 1996 and 1995 in numerical densities were taxonomically general (Tables 4, 5).

Length Frequency Composition

FFS

Relatively more young-of-the-year (YOY) and other small-bodied ($\leq 7\text{ cm}$) fish contributed to length frequency tallies in August 1996 compared to September 1995; overall there were 56% and 43% YOY-sized fishes tallied in August 1996 and September 1995, respectively. Between-year differences in the length

frequency distributions of fishes sampled in each major habitat and both habitats pooled (2-sample K-S tests, all $P < 0.01$; Fig. 1A,B) resulted from both relatively greater numbers of smaller (1-3 cm) YOY in 1995 and disproportionately more, larger (4-7 cm) YOY and yearling-sized (7-11 cm) fishes in 1996.

MWAY

Length frequency distributions differed between September 1996 and September 1995 in each and both habitats pooled (K-S tests, all $P < 0.01$; Fig. 2A,B). In all cases the 1995-96 differences represented relatively greater numbers of 4-5 cm YOY in 1995 and disproportionately more 7-11 cm yearlings in 1996. The overall contributions of YOY-sized (≤ 7 cm) fishes were 33% in both September 1996 and September 1995.

Biomass

FFS

In August 1996, mean biomass densities of total fishes were $0.5-0.6 \text{ kg} \cdot 10 \text{ m}^{-2}$, with herbivores comprising 37-65% and carnivores 35-63%, depending on habitat. These 1996 estimates appear smaller but are statistically equivalent to the respective September 1995 estimates for herbivores, carnivores, and total fishes (Fig. 3A). Variances are large (Fig. 3A) and statistical power is insufficient to resolve suggestions of change between years. YOY-sized fishes contributed only about 7% and 2% to total biomass on the 1996 and 1995 surveys, respectively.

MWAY

Biomass densities in September 1996 averaged $0.8-0.9 \text{ kg} \cdot 10 \text{ m}^{-2}$; about 21-68% were herbivores and 32-79% were carnivores, depending on habitat. Biomass estimates in 1996 were nominally smaller, but statistically indistinguishable from September 1995 values due to the large variances of both survey estimates (Fig. 3B). YOY-sized fishes represented only about 3% and 1% of total biomass in 1996 and 1995, respectively.

DISCUSSION

Temporal Comparisons of Relative Abundance

FFS and MWAY

The distributions of counts among taxa were fundamentally similar between the August (FFS)-September (MWAY) 1996 and the respective September 1995 survey. At FFS, the overall rank composition of species within the shallow reef fish assemblage has persisted despite quantitative changes in the abundance and size structure of reef fishes between July 1992 and September

1995 (DeMartini and Parrish, 1996) and more recent changes in size structure between September 1995 and August 1996. At MWAY, species rankings remained concordant along with numerical densities and size distributions from August 1993 to September 1995, and despite changes in size structure between September 1995 and September 1996. We continue to interpret these observations as indicating stability in fish assemblage structure at both FFS and MWAY.

Temporal Changes in Numerical Density

FFS

Equivalently high densities persisted from September 1995 to August 1996. Between July 1992 and September 1995, the numerical densities of shallow reef fishes had increased > 60% (DeMartini and Parrish, 1996). These increases had been spatially general--an estimated 37% on the barrier reef and 63% on patch reefs (DeMartini and Parrish, 1996)--indicating that numerical increases had occurred on larger-than-physiographic spatial scales (Sale et al., 1994). The similar 1995-96 estimates suggest that the numerical increases evident in 1995 have persisted for at least an additional 11 months (Fig. 4A).

MWAY

Like FFS, fish densities at MWAY remained similar between 1995 and 1996 (Fig. 4B). The magnitude of the 1996 estimates, relative to those of 1995, ranged broadly around no net change (from one-fourth less to one-half greater in 1996) among the two trophic levels and component feeding guilds examined. Total fish densities had nominally increased by 31% overall at MWAY between August 1993 and September 1995, but the increase was not statistically demonstrable (DeMartini and Parrish, 1996, Table 5).

General

Equivalent fish densities during 1995-96 at FFS and at MWAY suggest that, at least in terms of overall numbers, abundances at both sites are now persisting at levels higher than those that occurred during the late eighties and early 1990s (DeMartini et al., 1996; Fig. 4, this study), a period of lower productivity in the NWHI ecosystem (Polovina et al., 1995, 1996).

Temporal Patterns of Size Composition and Biomass

FFS

The observation that relatively greater numbers of YOY and other small-bodied (≤ 7 cm) fishes were tallied on the August 1996 vs September 1995 surveys is an overgeneralization that obscures two key facts: (1) relatively more older YOY and

yearlings were tallied in 1996, and (2) disproportionately more early YOY were tallied in 1995. Both (1) and (2) further attest to the strong 1995 year-classes first reported by DeMartini and Parrish (1996).

YOY had been relatively more numerous at FFS in September 1995 compared to July 1992 due to the strong 1995 year-classes of many species of shallow reef fishes (DeMartini and Parrish, 1996; E. DeMartini, unpubl. obs.). The relative increase in YOY between the 1992 and 1995 surveys (42%) was substantial. Although the 1995 increase in YOY counts was less than that necessary to explain the observed increase of > 60% in total fish density, the higher YOY counts in part contributed to the general increase in numbers. In 1995, YOY contributed only about 2% to the standing biomass of shallow reef fish at FFS (DeMartini and Parrish, 1996). Higher apparent biomass densities in 1995 reflected the greater numerical densities of larger-bodied fish that perhaps represented the grow-out of juveniles from successful year classes established between 1992 and 1995 (DeMartini and Parrish, 1996).

In 1996, YOY again contributed little to overall standing biomass. Biomass densities remained indistinguishable from 1995 despite the relative increase in 1996 of yearling-sized fish. This is not surprising because yearling-sized (7-11 cm) fish, although larger-bodied than YOY (1-7 cm, 0.1-12 g), averaged only about an ounce (27-32 g) per individual in 1996, depending on habitat. More than several highly successful year-classes in succession would be needed to appreciably increase standing biomass.

MWAY

The equivalent proportions of YOY-sized fish in August 1993 and September 1995 (31-33% of all fishes tallied) remained unchanged in September 1996 (33%), despite the observed 1995-96 changes in length frequency distributions. As at FFS, the changes in size composition occurred in both major habitats and comprised relative increases and decreases in yearlings and early YOY, respectively. The 1996 increase in yearlings suggests that successful 1995 year-classes also became established at MWAY, even though our 1995 estimates were too imprecise to adequately describe them. The geographic scope of reef fish recruitment success in 1995 may have extended farther upchain in the NWHI than we had originally surmised (DeMartini and Parrish, 1996).

As at FFS, the 1996 increases in yearling-sized fish failed to promote an increase in standing biomass that was detectable within the precision limits of a single survey. At present, our estimates of biomass density at MWAY (and FFS) indicate values that have broadly ranged around $1 \text{ kg} \cdot 10 \text{ m}^{-2}$ from 1992/3 through 1996 (DeMartini and Parrish, 1996; Fig. 3, this study).

General

Our estimates of fish biomass densities on shallow NWHI reefs of $1 \text{ kg} \cdot 10 \text{ m}^{-2}$ are about twice the average level of fish standing biomass on shallow reefs in the main Hawaiian Islands (MHI) (Grigg, 1994; DeMartini et al., 1996). We reemphasize the importance of these differences as evidence for the high present and continuing level of exploitation of reef fishes in the MHI.

SUMMARY AND CONCLUSIONS

At FFS, the numerical density of reef fishes (all taxa, both major habitats) in August 1996 was equivalent (mean \pm se = $16.8 \pm 4.0 \text{ fish} \cdot 10 \text{ m}^{-2}$) to the estimate made in September 1995 ($19.7 \pm 4.7 \text{ fish} \cdot 10 \text{ m}^{-2}$). At MWAY, the analogous estimate made in September 1996 ($19.2 \pm 4.6 \text{ fish} \cdot 10 \text{ m}^{-2}$) was equivalent to that made in September 1995 ($18.8 \pm 4.6 \text{ fish} \cdot 10 \text{ m}^{-2}$).

The length frequency distributions of fishes at FFS in August 1996 and at MWAY in September 1996 differed in similar fashion from the respective September 1995 estimates, reflecting relatively few early YOY (new recruits) together with relatively greater numbers of older YOY and yearling survivors of 1995 year-classes. At FFS, YOY and other small-bodied (1-7 cm) fishes were relatively more numerous in 1996 (56%) than in 1995 (43%) because of the greater contribution of older YOY in 1996. YOY and other small fishes comprised 33% of total fishes tallied at MWAY in September 1996, a value similar to analogous estimates for September 1995 (33%) and August 1993 (31%) because increases in yearling-sized (7-11 cm), not YOY-sized, fishes were observed at MWAY in 1996.

At FFS, estimates of standing biomass in 1996 ($0.5\text{-}0.6 \text{ kg} \cdot 10 \text{ m}^{-2}$) were indistinguishable from values estimated in 1995 ($0.7\text{-}1.9 \text{ kg} \cdot 10 \text{ m}^{-2}$) and in 1992 ($0.4\text{-}1.1 \text{ kg} \cdot 10 \text{ m}^{-2}$). Biomass estimates at MWAY in 1996 ($0.8\text{-}0.9 \text{ kg} \cdot 10 \text{ m}^{-2}$) were similar to those estimated at MWAY in 1995 (0.8 to $< 2 \text{ kg} \cdot 10 \text{ m}^{-2}$) and in 1993 ($1.0\text{-}1.1 \text{ kg} \cdot 10 \text{ m}^{-2}$). YOY again contributed little to overall biomass densities in 1996 at FFS (7%) and at MWAY (3%).

The increases in recruitment detected at FFS in September 1995 were initially interpreted by DeMartini and Parrish (1996) as perhaps the continuation of recent increases in reef fish numbers that had not yet fully translated to increased adult standing biomass. Length frequencies observed on the August 1996 (FFS) and September 1996 (MWAY) surveys suggest that, at both sites, the grow-out of successful 1995 year-classes has continued, but that recruitment in 1996 was relatively poor. Surveys over multiple years will be necessary to document the likely sporadic establishment of year classes, and the accrual of biomass by successful, sequential year-classes that would be necessary for substantial increases in the reef fish forage base.

at FFS. Temporal changes in reef fish abundance at MWAY need further documentation because of the importance of this site for potential translocation of seals. In general, the link between reef fish recruitment and production and meaningful increases in the reef fish component of the monk seal forage base still needs to be further described.

ACKNOWLEDGMENTS

We thank K. McDermond and M. Nishimoto, Hawaiian Islands National Wildlife Refuge, U.S. Fish and Wildlife Service, and LT K. Rinaldi, Midway Naval Air Station, for administrative support. We also thank J. Polovina and T. Ragen for constructive criticisms of a manuscript draft, and D. Yamaguchi for assistance with figures.

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Table 1.--FFS. Mean numerical densities ($N \cdot 10 \text{ m}^{-2}$) of major fish taxa on the September 1995 and August 1996 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each survey for both habitat types pooled. Trophic guild acronyms are: bc = benthic carnivores; h = herbivores; co = corallivores; zp = planktivores; pi = piscivores. A dashed horizontal line separates the top 30, 1995 taxa from lower-ranked taxa that ranked within the top 30 on the 1996 survey. abs = absent.

Taxon	September 1995				August 1996			
	Rank95	DBR	DPR	Dboth	Rank96	DBR	DPR	Dboth
<i>Mulloid. vanicolensis</i> (bc)	1	abs	8.83	4.41	2	.20	3.09	1.81
Juvenile Scaridae(h)	2	.64	3.53	2.25	6	.34	1.60	1.04
<i>Dascyllus albisella</i> (zp)	3	abs	3.47	1.73	1	.03	5.40	3.01
<i>Thalassoma duperrey</i> (bc)	4	.74	1.52	1.18	4	.88	1.53	1.24
<i>Chromis ovalis</i> (zp)	5	.30	1.79	1.12	10	.08	.77	.46
<i>Stegastes fasciolatus</i> (h)	6	.10	1.75	1.02	3	.32	2.48	1.52
<i>Ctenochaetus strigosus</i> (h)	7	.63	1.24	.97	5	.54	1.77	1.22
<i>Neoniphon sammara</i> (bc)	8	<.01	.96	.54	13	<.01	.56	.31
<i>Chromis vanderbilti</i> (zp)	9	1.00	.01	.45	11	.78	abs	.39
<i>Chaetodon miliaris</i> (zp)	10	.06	.76	.45	8	.04	1.27	.72
<i>Acanthurus triostegus</i> (h)	11	.20	.61	.43	12	.20	.53	.38
<i>Acanthurus</i> spp ^a (h)	12	.73	.19	.43	15	.34	.17	.25
<i>Mulloid. flavolineatus</i> (bc)	13	abs	.64	.32	7	abs	1.82	.91
<i>Chromis hanui</i> (zp)	14	>.36	.25	.30	18	.02	.31	.18
<i>Stethojulis balteata</i> (bc)	15	.17	.39	.29	17	.10	.28	.20
<i>Centropyge potteri</i> (h)	16	.08	.36	.24	16	<.01	.37	.21
<i>Scarus</i> spp ^b (h)	17	.26	.19	.22	9	.26	.75	.54
<i>Paru. multifasciatus</i> (bc)	18	.10	.29	.21	20	.10	.18	.15
<i>Lutjanus kasmira</i> (bc)	19	abs	.41	.21	14	.09	.41	.27
<i>Thalassoma ballieui</i> (bc)	20	.17	.21	.19	23	.09	.16	.13
<i>Canthigaster jactator</i> (bc)	21	>.08	.23	.16	22	.12	.15	.13
<i>Macrophar. geoffroy</i> (bc)	22	<.02	.27	>.15	24	.02	.21	.13
<i>Zebrasoma flavescens</i> (h)	23	.04	.20	.13	25	<.01	.21	.12
<i>Naso unicornis</i> (h)	24	>.02	.19	>.11	32	.03	.05	.05
<i>Cheilinus unifasciatus</i> (pi)	25	abs	.15	.08	44	<.01	.03	.02
<i>Chaetodon fremblii</i> (bc)	26	.03	.12	.08	28	.04	.11	.08
<i>Naso lituratus</i> (h)	27	>.02	.12	.08	36	.03	.07	.04
<i>Aulostomus chinensis</i> (pi)	28	abs	.15	.07	31	abs	.11	.06
<i>Bodianus bilunulatus</i> (bc)	29	.08	.07	.07	29	.07	.09	.08

Table 1.--FFS (continued).

Taxon	September 1995				August 1996			
	Rank95	DBR	DPR	Dboth	Rank96	DBR	DPR	Dboth
<i>Plectro. johnstonianus</i> (co)	30	.03	.11	.07	27	.01	.15	.09

<i>Kyphosus</i> spp	58	.02	abs	<.01	19	.32	abs	.16
<i>Labroides phthirophagus</i> (bc)	31	.03	.09	.07	21	.01	.25	.14
<i>Myripristis</i> spp	34	.01	.09	.06	26	.17	.06	.11
<i>Paru. pleurostigma</i> (bc)	36	abs	.11	.05	30	<.01	.11	.06
Top 10 taxa		5.0	24.5	14.1		4.2	20.5	12.5
Top 20 taxa		5.9	27.7	16.9		5.2	23.8	15.0
Top 30 taxa		6.2	29.1	18.0		5.5	25.0	16.1
Total fishes		6.4	30.4	19.7		5.6	25.8	16.8

^a*Acanthurus nigroris*, *A. nigrofuscus*, *A. blochii*, *A. xanthopterus*, *A. dussumieri*, and *A. olivaceus*

^b*Scarus* spp adults, including *S. perspicillatus* and *S. sordidus*

Table 2.--MWAY. Mean numerical densities ($N \cdot 10 \text{ m}^{-2}$) of major fish taxa on the September 1995 and September 1996 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each sampling period for both habitat types pooled. For trophic guild acronyms see Table 1 caption. A dashed horizontal line separates the top 30, 1995 taxa from lower-ranked taxa that ranked within the top 30 on the 1996 survey. September 1995 BR data include Station 10; data were not collected at Station 10 on the September 1996 survey.

Taxon	September 1995				September 1996			
	Rank95	DBR	DPR	Dboth	Rank96	DBR	DPR	Dboth
<i>Apogon</i> spp(zp)	1	abs	3.73	1.86	9	abs	1.11	.56
<i>Stegastes fasciolatus</i> (h)	2	1.34	1.88	1.64	3	2.20	2.68	2.50
<i>Chromis ovalis</i> (zp)	3	1.54	1.52	1.53	7	.55	.71	.65
<i>Paru. pleurostigma</i> (bc)	4	abs	2.84	1.42	8	<.01	1.02	.64
<i>Acanthurus triostegus</i> (h)	5	2.84	.21	1.38	20	.31	.04	.14
<i>Dascyllus albisella</i> (zp)	6	abs	2.62	1.31	4	abs	3.22	1.61
<i>Mulloid. flavolineatus</i> (bc)	7	.04	2.14	1.21	1	<.01	5.14	3.21
<i>Thalassoma duperrey</i> (bc)	8	>.64	1.15	.93	5	1.46	1.36	1.39
<i>Chaetodon miliaris</i> (zp)	9	<.02	1.50	.84	6	abs	1.99	.99
Juvenile Scaridae(h)	10	<.02	1.12	.63	2	.45	4.08	2.72
<i>Thalassoma ballieui</i> (bc)	11	>.34	.23	.28	11	.37	.16	.24
<i>Paru. porphyreus</i> (bc)	12	abs	.54	.27	30	<.01	.09	.06
<i>Kyphosus</i> sp(h)	13	.52	abs	.26	14	.33	.14	.21
<i>Coris venusta</i> (bc)	14	.04	.40	.24	17	.02	.28	.18
<i>Abudefduf abdominalis</i> (zp)	15	.08	.34	.22	12	.38	<.14	.23
<i>Cheilinus bimaculatus</i> (bc)	16	abs	.43	<.22	16	abs	.39	.19
<i>Acanthurus</i> spp ^a (h)	17	>.44	.01	.20	38	.09	abs	.04
<i>Scarus</i> spp ^b (h)	18	<.28	>.12	.19	18	.32	<.05	.15
<i>Chaetodon fremblii</i> (bc)	19	.02	.32	>.18	23	<.01	>.16	.10
<i>Stethojulis balteata</i> (bc)	20	.17	.16	.17	10	.47	.26	.34
<i>Canthigaster jactator</i> (bc)	21	.01	.27	.16	50	abs	<.03	.01
<i>Myripristis</i> spp(zp)	22	.22	.09	.15	27	abs	>.16	.08
Synodontidae(pi)	23	abs	.23	.11	26	abs	.16	.08
<i>Ctenochaetus strigosus</i> (h)	24	.09	>.11	.10	28	<.02	.11	.07
<i>Coris flavovittata</i> (bc)	25	<.06	.14	.10	49	.03	abs	<.02
<i>Dendrochirus barberi</i> (pi)	26	abs	.19	<.10	41	abs	<.09	>.04
<i>Acanthurus leucopareius</i> (h)	27	<.18	abs	.09	25	.20	abs	.10
<i>Adioryx</i> spp(bc)	28	<.01	.14	.08	72	<.01	abs	<.01
<i>Plectro. johnstonianus</i> (co)	29	>.06	<.09	<.08	35	.04	.05	<.05
<i>Paracirrhites forsteri</i> (bc)	30	abs	.11	.06	29	<.01	.11	.07

Table 2.--MWAY (continued).

Taxon	September 1995				September 1996			
	Rank95	DBR	DPR	Dboth	Rank96	DBR	DPR	Dboth
<i>Labroides phthirophagus</i> (bc)	43	.03	.03	.03	15	.05	.31	.21
<i>Neoniphon sammara</i> (bc)	52	abs	<.04	<.02	13	.01	.35	.22
<i>Paru. multifasciatus</i> (bc)	35	abs	.09	.04	19	abs	.30	.15
<i>Mulloid. vanicolensis</i> (bc)	--	abs	abs	abs	21	abs	.26	.13
<i>Aulostomus chinensis</i> (pisc)	33	abs	.10	.05	22	abs	.24	.12
<i>Chromis hanui</i> (zp)	38	.01	>.06	<.04	24	<.01	.16	.10
Top 10 taxa		8.3	19.0	12.8	6.8	21.7	14.6	
Top 20 taxa		9.1	21.8	15.0	7.5	24.2	16.6	
Top 30 taxa		9.4	22.9	16.0	7.7	25.4	17.5	
Total fishes		9.6	23.7	17.4	7.9	26.1	18.3	

^a*Acanthurus nigrofuscus* and/or *A. nigroris*^b*Scarus* spp adults, including *S. perspicillatus* and *S. sordidus*

Table 3.--FFS. Summary comparisons between September 1995 and August 1996 densities ($N \cdot 10 \text{ m}^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. All tests were evaluated at $\alpha_{\text{crit}} < \alpha_{2,0.10/m}$ with m's as defined in the Methods. Standard errors are listed in parentheses for the September 1995 means. Sample sizes are 4, 5 and 9 for BR, PR, and both habitats, respectively. (* indicates significance at $< \alpha_{2,0.10/m}$.) Tests for stations pooled over both habitats were considered "na" if trends for BR and PR stations were opposite.

Trophic level/guild	Reef type	SEP 1995 mean (se)	% total fishes	Change (%)	Prob. change=0
Total fishes	BR	6.5 (1.8)	100	- 12	--
	PR	30.4 (3.7)	100	- 11	--
	both	19.7 (4.7)	100	- 15	0.14
Herbivores	BR	2.8 (0.2)	43	- 11	--
	PR	8.4 (2.2)	28	- 4	--
	both	5.9 (1.5)	30	- 5	0.79
Secondary consumers	BR	3.7 (1.8)	57	- 14	--
	PR	22.0 (3.4)	72	- 19	--
	both	13.8 (3.8)	70	- 19	0.05 ns
benthic carnivores	BR	1.7 (0.3)	26	+ 9	0.68
	PR	14.5 (2.8)	48	- 38	<0.001 *
	both	8.8 (2.7)	45	- 34	na
planktivores	BR	1.8 (1.7)	27	- 36	ns
	PR	6.6 (0.8)	22	+ 19	ns
	both	4.4 (1.2)	22	+ 9	na
corallivores	BR	0.10(.05)	<2	- 45	ns
	PR	0.23(.06)	<1	+ 20	ns
	both	0.17(.05)	<1	+ 3	na
piscivores	BR	0.12(.08)	<2	+ 1	--
	PR	0.68(.35)	2	- 14	ns
	both	0.43(.21)	2	- 11	na

Table 4.--FFS and MWAY. Summary of nominal (signed) changes in density within the top 30 taxa of reef fishes, grouped by major trophic level and carnivore feeding guild, between the September 1995 and the August (FFS) or September 1996 (MWAY) surveys. Noted are results for binomial tests of the relative number of nominal increases and decreases.

	French Frigate Shoals		Midway Atoll	
	Increase	Decrease	Increase	Decrease
Herbivores	4	5	3	4
Secondary consumers	11	10	13	10
benthic carnivores	6	7	8	6
planktivores	3	3	4	3
corallivores	1	0	0	0
piscivores	1	0	1	1
Total fishes	15	15	16	14
Ho : # decreases = # increases				
H _{a2} : # decreases ≠ # increases				
15/30 increases			16/30 increases	
P≈1.0			P=0.86	

Table 5.--MWAY. Summary comparisons between September 1995 and September 1996 densities ($N \cdot 10 \text{ m}^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. Sample sizes are 3, 5 and 8 for BR, PR, and both habitats, respectively (September 1995 data for BR Station 10 are omitted from comparisons because Station 10 was not sampled in September 1996.) Other details are noted in the Methods and Table 3 caption.

Trophic level/guild	Reef type	SEP 1995 mean (se)	% total fishes	Change (%)	Prob. change=0
Total fishes	BR	10.5 (2.9)	100	- 25	--
	PR	23.7 (6.4)	100	+ 10	--
	both	18.8 (4.6)	100	+ 2	na
Herbivores	BR	6.5 (3.7)	62	- 38	ns
	PR	3.7 (0.6)	16	+ 96	ns
	both	4.7 (1.4)	25	+ 27	na
Secondary consumers	BR	4.0 (1.8)	38	- 4	--
	PR	20.0 (6.0)	84	- 6	--
	both	14.0 (4.7)	74	- 6	0.96
benthic carnivores	BR	1.8 (0.3)	17	+ 56	ns
	PR	9.6 (2.3)	40	+ 11	--
	both	6.7 (2.0)	36	+ 16	0.77
planktivores	BR	2.1 (2.1)	20	- 56	ns
	PR	9.9 (3.9)	42	- 24	ns
	both	7.0 (2.8)	37	- 28	0.59
corallivores	BR	0.13 (.07)	1	- 47	ns
	PR	0.12 (.05)	<1	- 41	ns
	both	0.12 (.04)	<1	- 44	0.24
piscivores	BR	0.00 (0.00)	0	-- ^a	--
	PR	0.40 (.23)	2	+ 23	--
	both	0.25 (.16)	1	+ 24	0.66

^aStatistically intractable

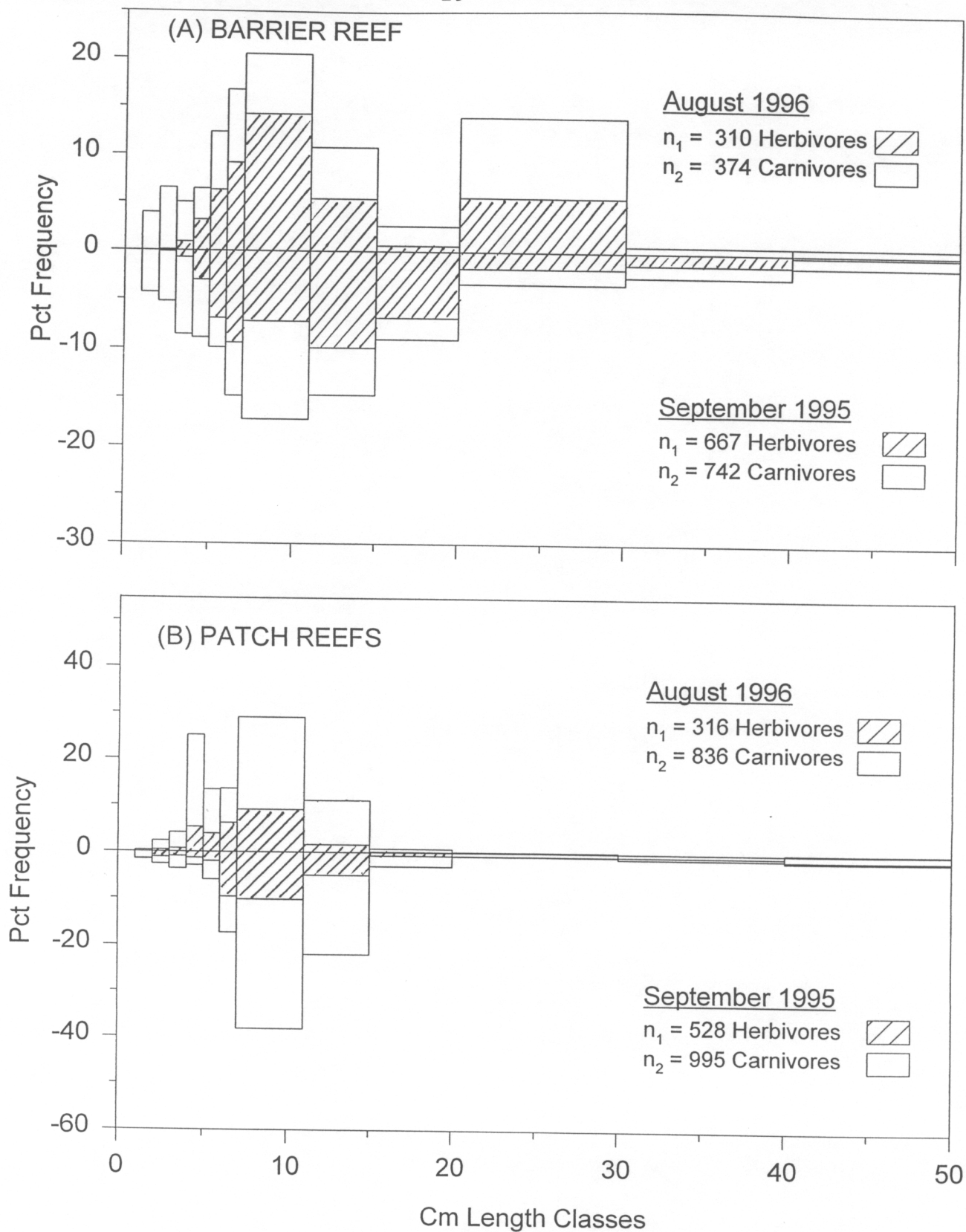


Figure 1.--French Frigate Shoals. Percentage frequency distributions of body length classes (cm SL) for herbivores (diagonal-right histograms) and carnivores (hollow histograms). Data for the barrier reef and patch reefs are plotted in panels A and B, respectively. In each panel, data for the August 1996 and September 1995 surveys are plotted above and below the horizontal axis, respectively.

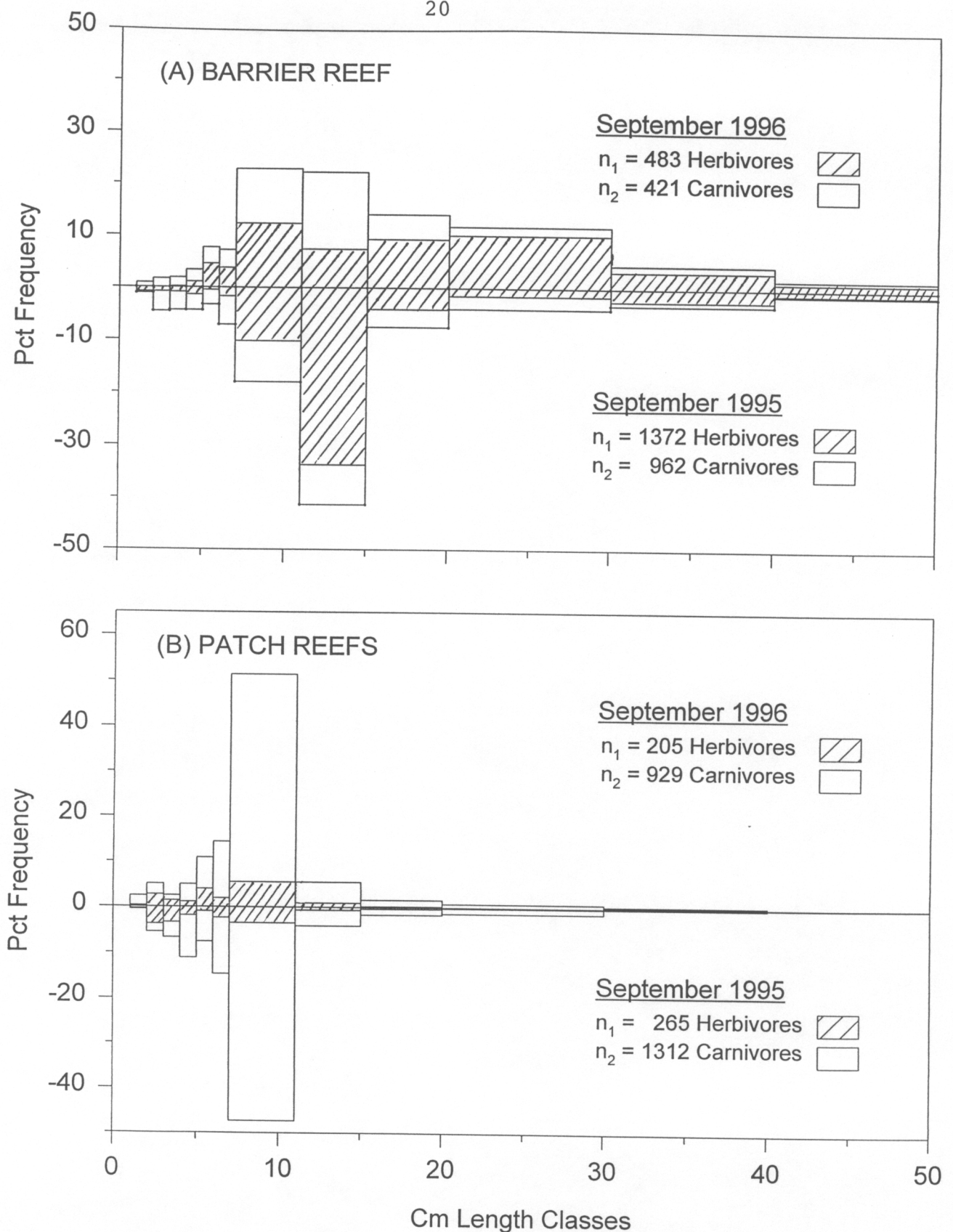


Figure 2.--Midway. Percentage frequency distributions of body length classes (cm SL) for herbivores and carnivores on the barrier reef (Panel A) and patch reefs (B), during the September 1996 (above x-axis) and September 1995 (below x-axis) surveys.

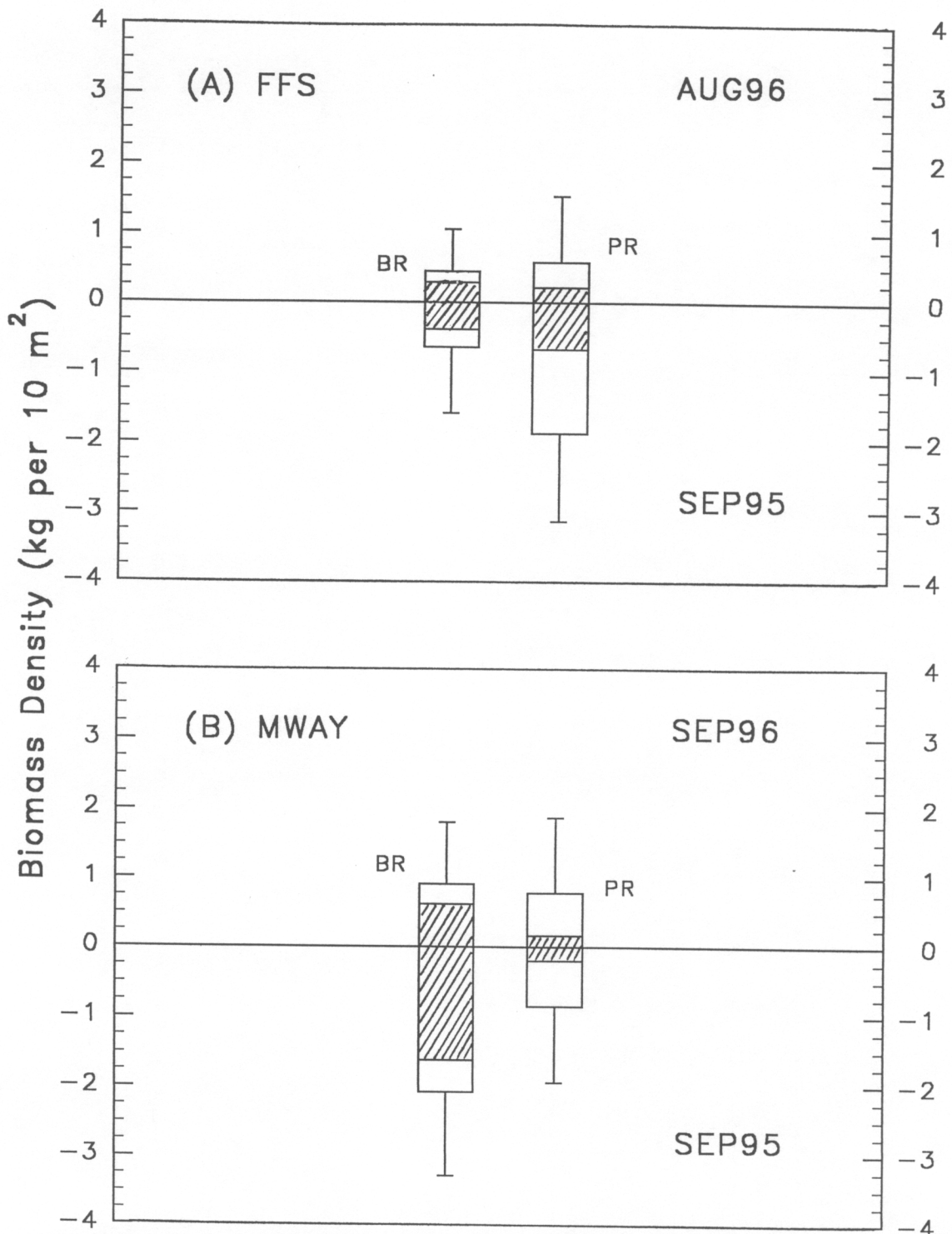


Figure 3.-- (A) French Frigate Shoals (FFS) and (B) Midway (MWAY). Estimated mean biomass densities (kg·10 m⁻²) of herbivores (diagonal-right histograms) and carnivores (hollow histograms), during surveys in August (FFS) and September 1996 (above x-axis) and in September 1995 at both FFS and MWAY (below x-axis). Also indicated is one approximately standard error of the biomass density of total (herbivore plus carnivore) fishes in each habitat during each survey.

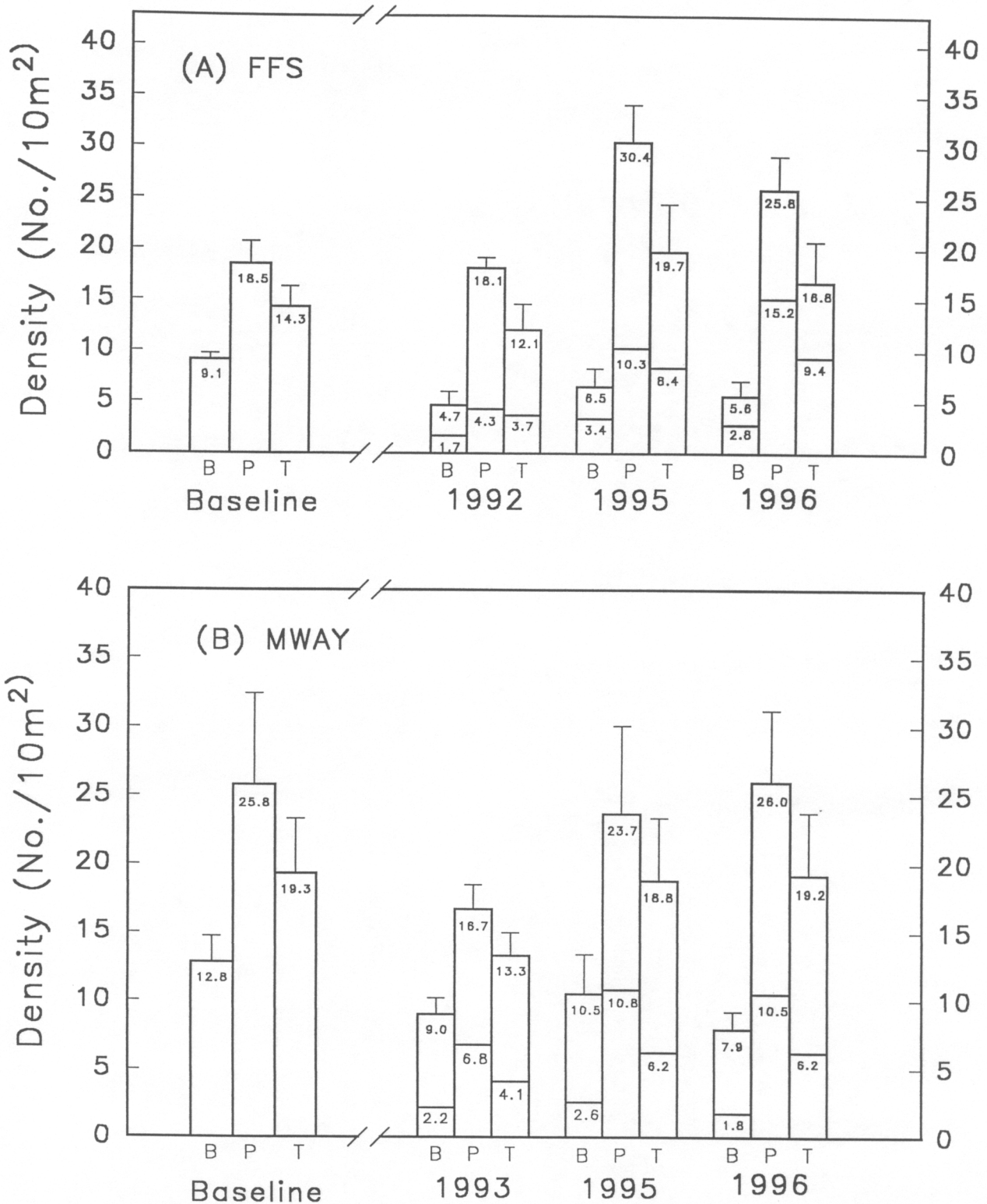


Figure 4.--(A) French Frigate Shoals (FFS) and (B) Midway (MWAY). Time series of the estimated numerical densities ($N \cdot 10^{-2}$) of total and YOY-sized (1-7 cm SL) fishes, at barrier (B), patch reef (P) and both habitats (T), during baseline, 1992 (FFS), 1993 (MWAY), 1995 (both sites), and 1996 (both sites) surveys. Baseline survey data were collected during 1980 and 1983 at FFS and during 1980 at MWAY (DeMartini et al., 1996). Vertical bar indicates 1 se of total fish density.